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Expanding the range of the troglobitic millipede *Pseudonannolene ambuatinga* Iniesta & Ferreira, 2013: insights into its distribution and conservation status (Spirostreptida, Pseudonannolenidae)

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Abstract. *Pseudonannolene* Silvestri, 1895 (Spirostreptida, Pseudonannolenidae) is one of the most common genera of millipedes in Brazilian caves. To date, only three troglobitic species are known in a list of 56 species described for the genus. In this study, we report new records of the cave-dwelling species *Pseudonannolene ambuatinga* Iniesta & Ferreira, 2013 in Minas Gerais state. These records extend its distribution by approximately 600 km^2, making it the most widely distributed cave-dwelling millipede in the country. We also provide a new assessment of its conservation status based on the records and threats to its populations.

Key words. Cave-dwelling, Grupo Bambuí, Myriapoda, Neotropics, Pains, troglomorphic

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INTRODUCTION

Pseudonannolene Silvestri, 1895 is the most diverse genus within the Neotropical Pseudonannolenidae Silvestri, 1895 (Spirostreptida), with 56 valid species (Iniesta et al. 2023a). Most of *Pseudonannolene* species are found in Brazil, with a considerable number of populations inhabiting areas associated with subterranean environments (Iniesta et al. 2023b). Over the past few decades, there has been an increasing interest in the taxonomy of this genus in Brazil, particularly concerning groups that are widely distributed in karst regions, including those regarded as obligatory cave-dwelling species (Iniesta and Ferreira 2013, 2014; Iniesta et al. 2023a, 2023b). To date, *Pseudonannolene* includes three troglobitic species (*sensu* troglobiont/troglobiotic species or population-race by Sket (2008)): *P. spelaea* Iniesta & Ferreira, 2013 found in iron-ore caves in Pará state; *P. ambuatinga* Iniesta & Ferreira, 2013 in carbonate caves in Minas Gerais state; and *P. lundi* Iniesta & Ferreira, 2020 from a single carbonate cave also in Minas Gerais state (for more details, see Iniesta et al. 2022, 2023a).

Identifying *Pseudonannolene* species as exclusively cave-dwelling solely based on distributional data is a challenging task because most of them, whether troglobitic or not, are found in karst regions. However, three of the 56 species known for the genus exhibit morphological adaptations associated with specific ecological restriction to caves: decrease in body size compared to related epigean species, body depigmentation in adults, and an apparent reduction in the number of ommatidia (observed only in *P. spelaea*) (Iniesta et al. 2023a). Physiological and biological adaptations related to the restriction to caves known for many other troglobiont invertebrate taxa are still undescribed for *Pseudonannolene* species, as well as for any other millipede in Brazil.

The troglobitic species *P. ambuatinga* was described in 2013 from caves in the Arcos-Pains-Doresópolis Speleological Unit, in Brazil (Iniesta and Ferreira 2013). It is characterized by the reduction of pigmentation (Figure 1), although preliminary tests revealed a gradual pigmentation for individuals exposed to light (Iniesta and Ferreira 2013). The species is restricted to the innermost areas of caves, with a clear preference for aphotic and highly humid environments, and with some individuals found completely submerged in water courses flowing inside the caves. They preferentially feed on bat guano and plant remains carried by water into the caves (Iniesta and Ferreira 2013).

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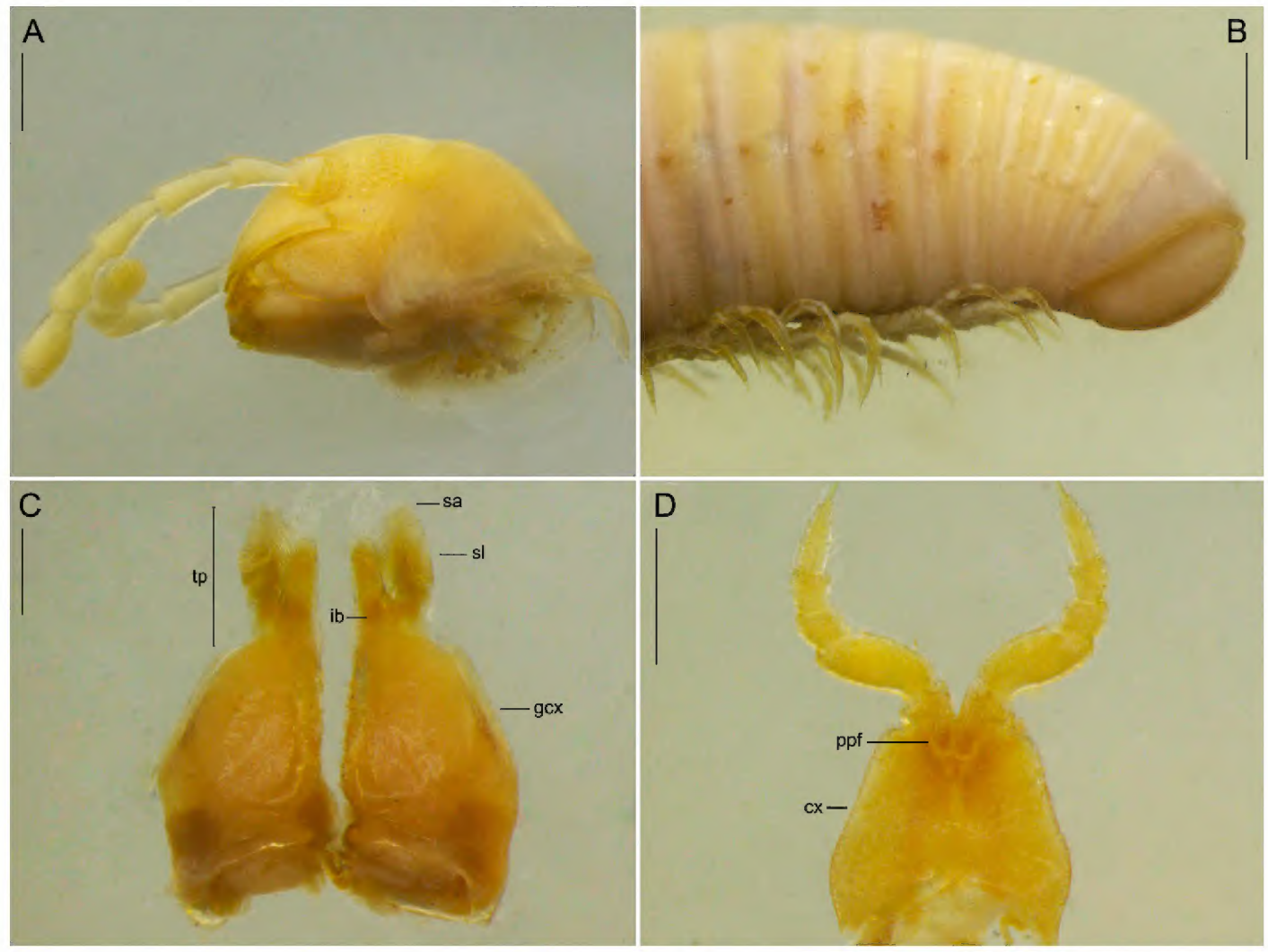

Figure 1. *Pseudonannolene ambuatinga* (IBSP 3442), male. **A.** Anterior region, lateral view. **B.** posterior region, lateral view. **C.** Gonopods, anal view. **D.** First leg-pair, oral view. Scale bars: 0.5 mm. Abbreviations: tp, telopodite; ib, internal branch; sa, seminal apophysis; sl, solenomere; gcx, gonocoxa; ppf, prefemoral process; cx, coxa.

According to the Red Book of Threatened Brazilian Fauna, *P. ambuatinga* is categorized as Endangered (ICMBio 2018) based on the IUCN Red List guidelines (Bland et al. 2017; Keith et al. 2013). The current classification resulted from the use of criteria B1ab(iii): extent of occurrence (EOO) <5,000 km^2 (B1); severely fragmented population or fewer than five locations (a), and with a continued decline in the number of locations or subpopulations (b[iii]). In this assessment, the extent of occurrence was estimated to be <100 km^2, considering the area between the two caves where the species has been recorded. The exhaustive mineral exploration in the region is the main threat and directly affects the species' habitat by potentially causing degradation to or even destruction of the caves (ICMBio 2018). The latest taxonomic review of the genus determined that *P. ambuatinga* has two junior synonyms: *P. saguassu* Iniesta & Ferreira, 2013, and *P. canastra* Gallo & Bichuette, 2020 (Iniesta et al. 2023a). The synonymization of these taxa added to the species' geographic distribution by providing additional occurrences (Iniesta et al. 2023a). Additionally, since its description, additional specimens have been found at new locations, which has resulted in considerable changes to the known distribution of *P. ambuatinga*.

The reassessment of conservation status due to taxonomic revision is expected within the framework of IUCN Red List under the category of "non-genuine reasons". This approach occurs when the species undergoes a taxonomic change, such as merging with other senior or junior synonyms, resulting in a broader range, larger population size, and other factors compared to previous assessments (IUCN 2023). After synonyms of *P. ambuatinga* have been identified and new records have been documented, it becomes imperative to consider these novel components into a new and updated assessment. This article aims to present a comprehensive overview of this species' distribution and conservation status by concerning data from all the caves from which samples have been obtained. It is hypothesized that *P. ambuatinga* may transition to a different Red List Category based on the emergence of synonyms and new occurrence records.

METHODS

The examined material is deposited in the following collections (curators in parenthesis): **IBSP**, Instituto Butantan, São Paulo, Brazil (A. D. Brescovit); and **ISLA**, Invertebrados Subterrâneos de Lavras, Minas Gerais, Brazil (R. L. Ferreira). Specimens were examined in 70% ethanol under a Leica MZ16A stereomicroscope and Leica DM400 microscope. Photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereomicroscope at the IBSP (São Paulo, Brazil). Focus-stacked images were composed with Leica Application Suite v. 2.5.0 (Leica Microsystems, Canton de Saint-Gall, Switzerland). All the specimen's identification and the terminology of sexual and somatic structures followed the taxonomic review provided by Iniesta et al. (2023a). The coloration patterns are described based on specimens preserved in 70–80% ethanol. The maps were obtained based on the species records in caves from São Roque de Minas-MG provided by Gallo and Bichuette (2020) and in the Arcos-Pains-Doresópolis speleological unit by Iniesta et al. (2023a), in addition to those of the material examined in the present study. The geographical coordinates were obtained from original labels of examined lots in the collections (when provided) and checked

individually according to the "Cadastro Nacional de Informações Espeleológicas (CANIE)". All the coordinates are shown in the South American Datum (SAD69).

The assessment of criteria and threat category for *Pseudonannolene ambuatinga* adheres to the IUCN Red List guidelines (Keith et al. 2013; Bland et al. 2017). Geographical coordinates of caves where the specimens originate were employed to delineate the species' distribution. The extent of occurrence (EOO) was determined by calculating the area (km^2) of a minimum convex polygon, the smallest polygon encompassing all known occurrences, ensuring no internal angle exceeded 180°, as indicated by Bland et al. (2017). In the assessment of threats, actions that could seriously and plausibly affect individuals of the species are listed. Disturbances and impacts in the karstic region where *P. ambuatinga* occurs are determined from the literature (Piló and Cruz 2022; Timo 2022). Once identified, these alterations were overlaid onto occurrences to ascertain the number of threat-defined locations. Maps were generated using data from the Atlas Digital Geoambiental (Instituto Prístino 2024), which were applied to determine the current threat category of *P. ambuatinga*.

RESULTS

Family Pseudonannolenidae Silvestri, 1895
Subfamily Pseudonannoleninae Silvestri, 1895
Genus *Pseudonannolene* Silvestri, 1895

Pseudonannolene ambuatinga Iniesta & Ferreira, 2013

Pseudonannolene ambuatinga Iniesta and Ferreira 2013: 358, figs 1–6.
Pseudonannolene saguassu Iniesta and Ferreira 2013: 363, figs 7–10; Iniesta et al. 2023a: 22 (syn.).
Pseudonannolene canastra Gallo & Bichuette 2020: 37, figs 3–6; Iniesta et al. 2023a: 22 (syn.).

Figure 1

Material examined. BRAZIL – Minas Gerais • Arcos, cave Alinhamento; −20.2891, −45.5401; 01.VI.2002; R. L. Ferreira leg.; 1 ♂, IBSP 3442 • cave S2-CRH-053; −20.3234, −45.5812; 06.XI–13.XII.2018; Equipe Spelayon leg.; 1 ♂, IBSP 11247 • cave S2-CRH-0106; −20.3300, −45.5816; same data as for preceeding; 1 ♂, IBSP 11380 • cave S2-CRH-0194; −20.3377, −45.5744; same data as for preceeding; 1 ♂, IBSP 12844 • cave Arcaica; −20.2868, −45.7933; 25.I.2008; E. O. Machado & J. P. P. Barbosa leg.; 1 ♀, IBSP 3317 • Iguatama, cave JAT28; −20.2888; −45.8159; 04.XII.2022; 1 ♀, IBSP 14641 • cave JAT17; −20.2872, −45.8156; 26.XI.2022; 1 ♀, IBSP 14634 • cave JAT42; −20.2866, −45.8187; 27.XI.2022; 2 juveniles, IBSP 14635 • cave JAT125; −20.2872; −45.8174, 04.XII.2022; 1 ♂ and 1 juvenile, IBSP 14643 • cave JAT84; −20.2871, −45.8165; 27.XI.2022; 1 juvenile, IBSP 14647 • cave JAT83; −20.2872, −45.8162; 27.XI.2022; 1 ♀, IBSP 14642 • cave JAT31; −20.2878, −45.8168; 25.XI.2022; 1 juvenile, IBSP 14640 • cave JAT11; −20.2834, −45.8170; 01.XII.2022; 1 ♀, IBSP 14636 • cave JAT21; −20.2876, −45.8153; 26.XI.2022; 2 juveniles, IBSP 14639 • cave JAT06; −20.2856, −45.8140; 16.XII.2022; 1 juvenile, IBSP 14632 • cave JAT34; −20.2880, −45.8163; 01.XII.2022; 1 juvenile, IBSP 14646 • cave JAT108; −20.2885, −45.8135; 30.XII.2022; all material collected by R. Zampaulo & A. S. Reis; 1 juvenile, IBSP 14644 • Pains, cave MIC033; −20.4285, −45.6220; 16.XI–11.XII.2015; Equipe Spelayon leg.; 1 ♀, IBSP 12177 • cave AGR006; −20.3417, −45.5753; 13.XI–14.XII.2015; Equipe Spelayon leg.; 1 ♀, IBSP 12266 • cave Escaravelho; −20.3970, −45.5824; VII.2008; E. O. Machado & J. P. P. Barbosa leg.; 1 juvenile, IBSP 3536 • cave Buraco do Katê; −20.3284, −45.8099; 28.XI.1999; R. L. Ferreira leg.; 1 ♀, IBSP 3594 • cave São Lourenço; −20.3284, −45.8099; 22.V.1999; R. L. Ferreira leg.; 1 ♀, IBSP 3598 • cave Capão Ducal; −20.3284, −45.8099; 05.V.2001; R. L. Ferreira leg.; 2 juveniles, IBSP 3587 • cave GA034; −20.3545, −45.8424; 05.II.2023; 2 ♂ and 1 juvenile, IBSP 14442 • cave GA236; −20.3533, −45.8405; 06.II.2023; 1 ♂, IBSP 14709 • cave GA337; −20.3547, −45.8424; 05.II.2023; 1 ♂, IBSP 14710 • cave GA360; −20.3579, −45.8400; 27.I.2023; 1 ♂, IBSP 14708 • cave GA395; −20.3544, −45.8408; 27.I.2023; 1 ♂, 1 ♀ and 1 juvenile, IBSP 14706 • cave GA014; −20.3516, −45.8459; 28.I.2023; 1 juvenile, IBSP 14633 • cave GA026; −20.3532, −45.8436; 09.II.2023; 3 juveniles, IBSP 14443 • cave GA034; −20.3545, −45.8424; 05.II.2023; 2 juveniles, IBSP 14442 • cave GA190; −20.3584; −45.8402; 27.I.2023; 1 juvenile, IBSP 14444 • cave GA192; −20.3577; −45.8396; 27.I.2023; 2 juvenile, IBSP 14631 • cave GA199; −20.3571, −45.8403; 28.i.2023; 1 juvenile, IBSP 14427 • cave GA281; −20.3482, −45.8449; 26.I.2023; 1 juvenile, IBSP 14441 • cave GA395; −20.3544, −45.8408; 27.I.2023; 1 juvenile, IBSP 14437 • cave GA401; −20.3543, −45.8413; 02.II.2023; 2 juveniles, IBSP 14434 • cave GA406; −20.3545, −45.8419; 03.III.2023; 1 juvenile, IBSP 14435 • cave GA409; −20.3539, −45.8412; 02.II.2023; 1 juvenile, IBSP 14430 • cave GA414; −20.3526, −45.8459; 08.IV.2023; 2 juveniles, IBSP 14431 • cave GA417; −20.3534, −45.8403; 06.II.2023; 1 juvenile, IBSP 14637 • cave GA437; −20.3485, −45.8501; 24.I.2023; 1 juvenile, IBSP 14440 • cave GA443; −20.3504, −45.8479; 28.I.2023; 1 juvenile, IBSP 14436 • cave GA449; −20.3561, −45.8409; 09.II.2023; 1 juvenile, IBSP 14439 • cave GA034; −20.3545, −45.8424; 31.VII.2023; 1 juvenile, IBSP 14442 • cave GA338; −20.3596; −45.8391; 20.V.2023; 1 juvenile, IBSP 14428 • cave GA364; −20.3556, −45.8400; 13.VII.2023; 1 juvenile, IBSP 14432 • cave GA390; −20.3560, −45.8413; 25.V.2023; 1 juvenile, IBSP 14438 • cave GA397; −20.3544, −45.8413; 29.VII.2023; 1 juvenile, IBSP 14433 • cave GA406; −20.3546, −45.8419; 27.VII.2023; all material collected by R. Zampaulo

& A. S. Reis; 1 juvenile, IBSP 14435 • cave do Abutre; −20.4003; −45.5719; 24.V.2019; F. Bondezan leg.; 1 ♀, IBSP 13356 • cave SF-694E; −20.3977, −45.5784; 25.III.2019; F. Bondezan leg.; 1 ♀, IBSP 13358 • cave SD−61E; −20.3941, −45.5693; 28.II.2019; F. Bondezan leg.; 1 juvenile, IBSP 13357 • cave SF-695C; −20.3976, −45.5780; 19.XI.2019; F. Bondezan leg.; 1 ♀, IBSP 13361 • cave Abismo Grande; −20.3978, −45.5765; 11.IX.2019; F. Bondezan leg.; 1 juvenile, IBSP 13362 • cave SF-657D; −20.4011, −45.5756; 06.VI.2019; F. Bondezan leg.; 1 juvenile, IBSP 13360 • cave Abismo da Bromélia 2; −20.4012; −45.5754; 26.VII.2019; F. Bondezan leg.; 1 ♀, IBSP 13363 • cave SF 1158 P; −20.3976, −45.5727; 30.X.2019; F. Bondezan leg.; 1 juvenile, IBSP 13359 • Piumhi, cave GA300; −20.3478, −45.8482; 06.VII.2022; R. Zampaulo & A. S. Reis leg.; 1 ♂, IBSP 14638.

Identification. Adults of *Pseudonannolene ambuatinga* resemble those of the troglobitic species *P. lundi* and *P. spelaea* by having head, trunk, and legs depigmented (Figure 1), but males can be distinguished by having a subtriangular solenomere (Figure 1C) vs. squared in *P. lundi* (Iniesta et al. 2023a: fig. 86D–F), a solenomere with the seminal apophysis evident (Figure 1C), and the number of ommatidia (ca. 25) vs. seminal apophysis covered by squamous membrane and around of 10 ommatidia in *P. spelaea* (Iniesta et al. 2023a: fig. 127A).

Conservation status. Currently the species is known from 59 limestone caves in the karst region of the municipalities of Arcos, Iguatama, Pains, Piumhi (Iniesta and Ferreira 2013; Iniesta et al. 2022), and São Roque de Minas (Gallo and Bichuette 2020).

The estimated area for the occurrence of *P. ambuatinga* is 608 km^2 (Figure 2). This region is located within the Cerrado biome near the border with the Atlantic Forest. The phytophysiognomies in the area include forest formations, open landscapes, and aquatic ecosystems. However, the landscape exhibits high fragmentation due to anthropogenic activities such as extensive livestock farming, cultivation of regional crops (e.g. beans and corn), and mineral extraction. The most significant threats identified include habitat loss (resulting from cave suppression), and alterations in habitat quality (due to agricultural activities around the cavities). Cave suppression primarily occurs to attend mineral extraction processes to obtain cement and its derivatives, a prevalent economic activity in this region.

Currently *P. ambuatinga* occurs in 10 caves situated within areas designated for mineral exploration, making them susceptible to future mining activities subject to environmental licensing (Figure 3). Additionally, two caves are currently located within protected areas, including Monumento Natural Jardim do Éden (Pains/MG) and Reserva Particular do Patrimônio Natural Serra dos Varões (Arcos/MG) (Figure 3). Moreover, the overall region exhibits a notable expansion of agricultural frontiers, resulting in the replacement of natural vegetation surrounding caves by grassland/pasture and cultivated/exposed soil.

The species distribution is now interpreted across 15 semi-independent threat-defined locations (Figure 3), which encompass mining titles (threats by habitat destruction), farms (threats by changes in habitat quality), and protected areas (currently without serious plausible threats). The new occurrences extend the known species locations beyond the established threat thresholds (Criterion B), despite a continued observed decline in habitat quality. As a result, the conservation status of *P. ambuatinga* aligns with the category of Near Threatened (NT), pending decisions by technical consultations and plenary sessions on

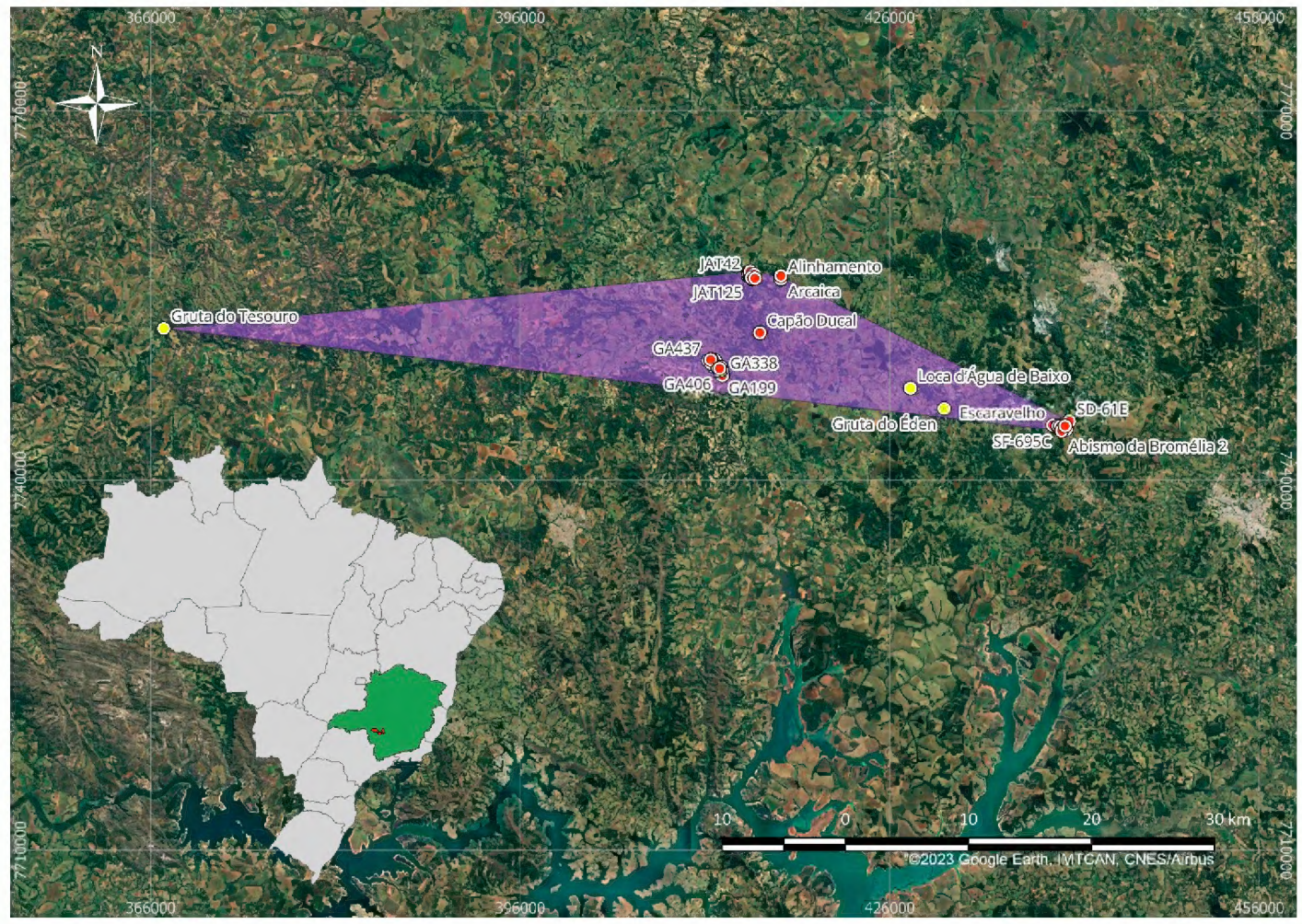

Figure 2. Geographic distribution of *Pseudonannolene ambuatinga* in Minas Gerais state, Brazil. The red points refer to the caves where the species occurs, the yellow points refer to the type localities of *P. ambuatinga* and of its synonyms, and the purple polygon represents its extent of occurrence. The geographic coordinates at the margins are expressed in UTM. Satellite image source: Google Earth 2023.

conservation policies. Nevertheless, it is highly recommended to pay special attention to the populations in caves that are not located in protected areas (Figure 3).

DISCUSSION

Our results present new perspectives for the conservation of *Pseudonannolene ambuatinga*, establishing it as the most widespread troglobitic species of the genus, even among all other cave-dwelling millipedes in Brazil. The new occurrence records expand the distribution of this troglobitic species from two to at least 59 caves. These caves comprise at least 15 threat-defined locations and, therefore, support a possible update to the species' conservation status to Near Threatened. Despite the positive news, we highlight the trend towards new mining ventures and expanded agriculture in the region. In the absence of effective preservation measures, these factors may lead the species' conservation status being reclassified in a threatened category in the future.

The concentration of occurrences in caves within the karst region of Pains highlights its local significance and the potential for new records. More than 2,500 caves are known in this area, making it the

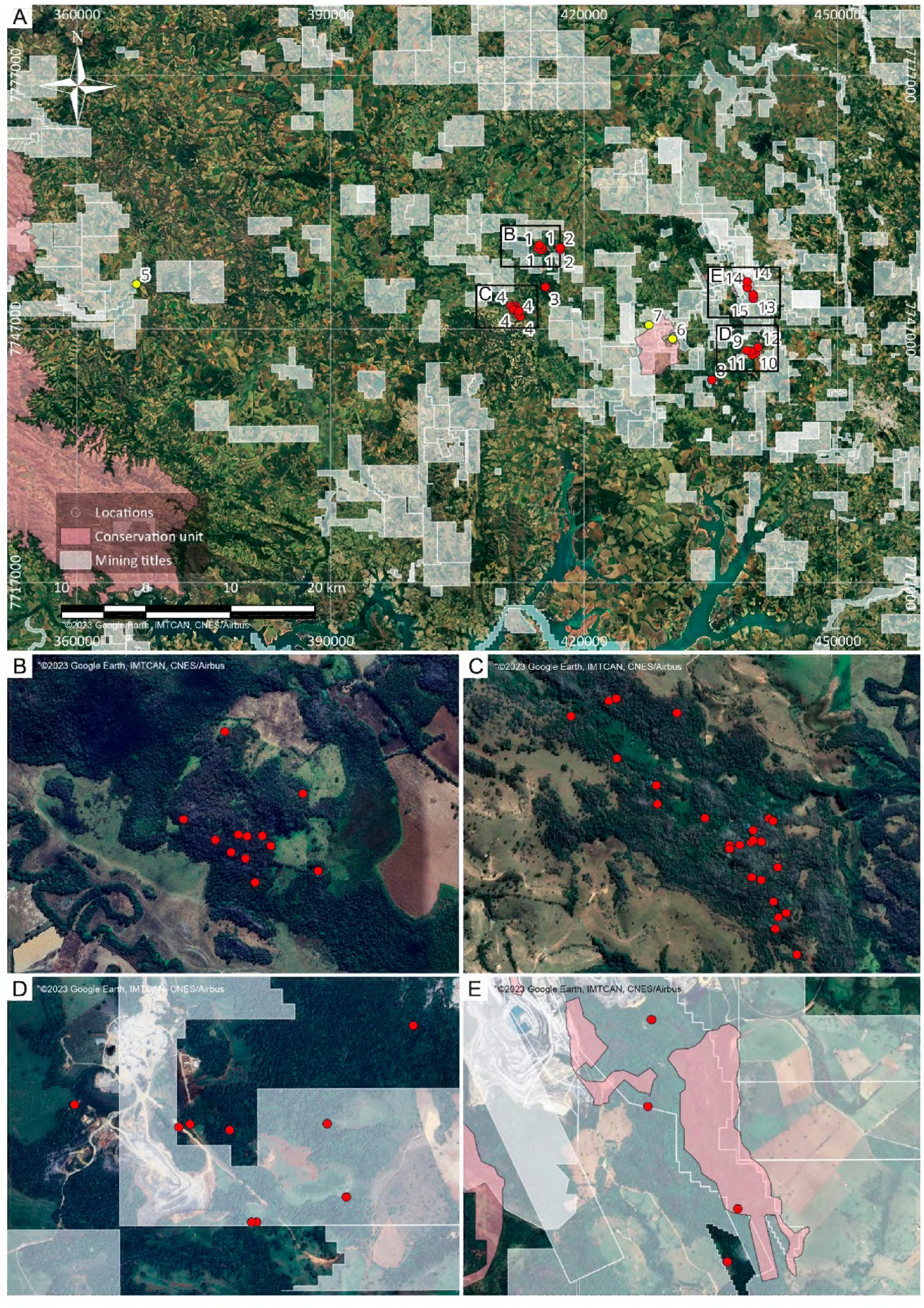

Figure 3. Threat-defined locations for *Pseudonannolene ambuatinga*. The red points refer to the caves where the species occurs, and the yellow points refer to the type localities of *P. ambuatinga* and of its synonyms**. A.** Overview of caves regarding the threat of habitat loss due to mining (mining titles in white) and permanent protection areas (conservation units in red). **B–E.** Caves in close proximity facing similar threats (or under full protection) were grouped as a single threat-defined location. The yellow points and numbers refer to the caves where the species occur. The geographic coordinates at the margins are expressed in UTM. Satellite image source: Google Earth 2023.

primary concentration of caves in South America (Frigo et al. 2022). Moreover, this karst region is situated in a transitional area between the biodiversity hotspots Cerrado (Brazilian savannah) and Atlantic Forest, which encompass regions regarded as areas of endemism for Spirostreptida species in the country (Iniesta et al. 2023b, 2023c). However, there is a scarcity of publications regarding cave-dwelling species in the region (Ferreira et al. 2022). Cave fauna inventories for environmental licensing processes of mining activities cover only small portions of the region and are conducted independently, both spatially and temporally. In addition, these inventories usually do not cover external areas surrounding the caves, which may contain a poorly known millipede fauna. Therefore, there is substantial potential for new records of *P. ambuatinga* as more studies are conducted.

While most caves in the region are typically dry and may not offer a suitable habitat for the establishment of millipede populations, observations of specimens have been limited to caves that have water sources (active at least part of the year) from percolating water, streams, or phreatic levels. Moreover, substantial populations of this species have been found in caves housing subterranean rivers, such as the Éden cave. According to Iniesta and Ferreira (2013), the species has consistently been found in aphotic areas within all caves where it occurs, indicating a clear preference for extremely humid environments far from cave entrances. It is not uncommon to see individuals completely submerged in the local streams within these caves. Also, specimens of *P. ambuatinga* did not exhibit any reaction to light, indicating a potential absence of phototaxy. This finding partially aligns with the study conducted by Gallo and Bichuette (2017), in which the light response of certain troglophile *Pseudonannolene* species showed a negative correlation with the number of ommatidia and ocular area. In the case of *P. ambuatinga*, anecdotal observations suggest a distinct preference for aphotic areas, with some specimens actively burying themselves in sediments and remaining there. It is crucial to emphasize that suitable habitats for this species would likely encompass aphotic areas characterized by high humidity levels. On the other hand, the phenology of the species is still far from being well understood, requiring further ecological studies to comprehend the relationship between local environmental conditions (e.g., luminosity, humidity, and organic sources) and the occurrence of *P. ambuatinga*.

The expansion of the species' range does not alleviate concerns about the substantial local anthropogenic threats. Limestone mining represents a significant economic activity in the region, which explored area have expanded by more than 151% between the 1980s and 2000s (Muniz and Fernandes 2013). This process results in the removal of rock matrices from limestone outcrops, leading to the suppression of cavities. Secondary activities associated with calcination can also lead to contamination and toxicity of aquifers, surface waters, as well as surface and underground ecosystems (Sanguinetto et al. 2018). In addition to mining, it is noteworthy that land use changes in the region indicated a significant expansion of agricultural frontiers between 2013 and 2020, reducing 40% of areas covered by natural vegetation (Galvão and Costa 2022). Given that resources in these caves originate from the nearby surface ecosystems (due to the constant absence of light, making underground primary productivity impossible), land use changes may reduce the quantity and quality of imported trophic items (Souza-Silva et al. 2011). Furthermore, they can alter the microclimatic conditions of these environments, including temperature, humidity, and water availability (Badino 2010), important environmental factors for the occurrence of *P. ambuatinga*. In conclusion, advances in the taxonomic study of *P. ambuatinga* have enabled the detection of new potential habitats for the species, facilitating updates to its conservation status and threat level. However, public policies must intervene in these areas to preserve subterranean habitats. Finally, we suggest that future studies should focus on ecological aspects, such as distribution patterns and population structure, and behavioral aspects, such as seasonal habitat occupancy responses. These are essential for the development of effective conservation and management strategies.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions
Conceptualization: LFMI, MPAO, RSB. Data curation: LFMI, MPAO, RSB. Formal analysis: MPAO. Funding acquisition: LFMI, MPAO, ADB, RSB. Investigation: LFMI, MPAO. Methodology: LFMI, MPAO. Resources: LFMI, MPAO, RSB. Supervision: ADB. Visualization: LFMI, MPAO, ADB, RSB. Project administration: LFMI, MPAO. Software: LFMI, MPAO. Validation: LFMI, MPAO, ADB, RSB. Writing – original draft: LFMI, MPAO, RSB. Writing – review and editing: LFMI, MPAO, ADB, RSB.

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Data availability
All data that support the findings of this study are available in the main text.

REFERENCES

Badino G (2010) Underground meteorology. What's the weather underground? Acta Carsologica 39: 427–448. https://doi.org/10.3986/ac.v39i3.74

Bland LM, Keith DA, Miller RM, Murray NJ, Rodríguez JP (2017) Guidelines for the application of IUCN Red List of Ecosystems Categories and Criteria, version 15.1. International Union for the Conservation of Nature, Gland, Switzerland, 114 pp. https://doi.org/10.2305/iucn.ch.2016.rle.3.en

Ferreira RL, Bernard E, da Cruz-Júnior FW, et al. (2022) Brazilian cave heritage under siege. Science 375: 1238–1239. https://doi.org/10.1126/science.abo1973

Frigo FJG, Sena FS, Assunção LN (2022) As cavernas da região cártisca de Pains. In: Piló LB, Cruz JB (Eds.) A região cárstica de Pains. ICMBio, Brasília, Brazil, 125–149.

Gallo JS, Bichuette ME (2017) Is there correlation between photophobia and troglomorphism in Neotropical cave millipedes (Spirostreptida, Pseudonannolenidae)? Zoomorphology 137 (2): 273–289. https://doi.org/10.1007/s00435-017-0389-0

Gallo JS, Bichuette ME (2020) *Pseudonannolene canastra* sp. nov. (Diplopoda, Spirostreptida) – A new troglobitic millipede from the southwestern state of Minas Gerais, Brazil. Subterranean Biology 35: 33–47. https://doi.org/10.3897/subtbiol.35.51183

Galvão P, Costa F (2022) Impactos ambientais, vulnerabilidade e ações de conservação na região cárstica de Pains. In: Piló LB, Cruz JB (Eds.) A região cárstica de Pains. ICMBio, Brasília, Brazil, 231–251.

ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VII – Invertebrados. ICMBio, Brasília, Brazil, 730 pp.

Iniesta LFM, Ferreira, RL (2013) Two new species of *Pseudonannolene* Silvestri, 1895 from Brazilian limestone caves (Spirostreptida: Pseudonannolenidae): synotopy of a troglophilic and a troglobiotic species. Zootaxa 3702 (4): 357–369. https://doi.org/10.11646/zootaxa.3702.4.3

Iniesta LFM, Ferreira, RL (2014) New species of *Pseudonannolene* Silvestri, 1895 from Brazilian limestone caves with comments on the potential distribution of the genus in South America (Spirostreptida: Pseudonannolenidae). Zootaxa 3846 (3): 361–397. https://doi.org/10.11646/zootaxa.3846.3.3

Iniesta LFM, Bouzan RS, Souza CAR (2022) Diplopoda. In: Zampaulo RA, Prous X (Eds.) Fauna cavernícola do Brasil. Rupestre, Minas Gerais, Brazil, 264–282.

Iniesta LFM, Bouzan RS, Brescovit AD (2023a) A reassessment of the Neotropical genus *Pseudonannolene* Silvestri, 1895: cladistic analysis, biogeography, and taxonomic review (Spirostreptida: Pseudonannolenidae). European Journal of Taxonomy 867: 1–312. https://doi.org/10.5852/ejt.2023.867.2109

Iniesta LFM, Bouzan RS, Brescovit AD (2023c) Spatial distribution and faunal composition of millipedes of the family Spirostreptidae Brandt, 1833 in the Brazilian Atlantic Forest (Diplopoda, Juliformia, Spirostreptida). Anais da Academia Brasileira de Ciências 95 (1): e20201937. https://doi.org/10.1590/0001-3765202320201937

Iniesta LFM, Bouzan RS, Means JC, Ivanov K, Brescovit AD (2023b) Where are they from and where are they going? Detecting areas of endemism, distribution patterns and conservation status of the order Spirostreptida in Brazil (Diplopoda, Juliformia). Biodiversity and Conservation 32: 1591–1615. https://doi.org/10.1007/s10531-023-02566-2

Instituto Prístino (2024) Atlas Digital Geoambiental. Instituto Pristino, Belo Horizonte, Brazil. https://institutopristino.org.br/atlas/. Accessed on: 2024-2-5.

IUCN (2023) The IUCN Red List of Threatened Species - Reasons for Changing Category, Cambridge, UK. https://www.iucnredlist.org/assessment/reasons-changing-category. Accessed on: 2024-2-5.

Keith DA, Rodríguez JP, Rodríguez-Clark KM, Nicholson E, et al. (2013) Scientific foundations for an IUCN Red List of Ecosystems. PLoS ONE 8 (5): e62111. https://doi.org/10.1371/journal.pone.0062111

Muniz F, Fernandes E (2013) Análise da expansão das áreas de cavas de mineração nos municípios de Arcos e Pains (MG) utilizando imagens Landsat. In: Anais do 32° Congresso Brasileiro de Espeleologia, Barreiras, Brasil, 239–244.

Piló LB, Cruz JB (2022) A região cárstica de Pains. ICMBio, Brasília, Brazil, 280 pp.

Sanguinetto E, Daniel GO, Ferreira MD (2018) Inclusão de áreas de proteção em feições cársticas e inovação minerária no município de Pains, MG. Caderno Prudentino de Geografia 40 (1): 68–92.

Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42: 1549–1563. https://doi.org/10.1080/00222930801995762

Souza-Silva M, Martins RP, Ferreira RL (2011) Trophic Dynamics in a Neotropical Limestone Cave. Subterranean Biology 9: 127–138. https://doi.org/10.3897/subtbiol.9.2515

Timo MB (2022) Caracterização geomorfológica da região cárstica Arcos-Pains e de seus sistemas cársticos. Caderno de Geografia 32 (68): 191–218. https://doi.org/10.5752/P.2318-2962.2022v32n68p191